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Abstract

1. Climate change is reported to have caused widespread changes to species' populations and ecological communities. Warming has been associated with declines in long-distance migrants, reductions in habitat specialists and increases in southerly distributed species. However, the specific climatic drivers behind these changes remain undescribed.

2. We analysed annual fluctuations in the abundance of 59 breeding bird species in England over 45 years to test the effect of monthly temperature and precipitation means upon population trends.

3. Strong positive correlations between population growth and both winter and breeding season temperature were identified for resident and short-distance migrants. Lagged correlations between population growth and both summer temperature and precipitation identified for the first time a widespread negative impact of hot, dry summer weather, whilst resident populations appeared to increase following wet autumns. Populations of long-distance migrants were negatively affected by May temperature, consistent with a potential negative effect of phenological mismatch upon breeding success. There was some evidence for non-linear relationships between monthly weather variables and population growth.

4. Habitat specialists and cold-associated species showed consistently more negative effects of higher temperatures than habitat generalists and southerly-distributed species associated with warm temperatures, suggesting that previously reported changes in community composition represent the accumulated effects of spring and summer warming.

5. Long-term population trends were more significantly correlated with species' sensitivity to temperature than precipitation, suggesting that warming had had a

greater impact on population trends than changes in precipitation. Months where there had been the greatest warming were the most influential drivers of long-term change. There was also evidence that species with the greatest sensitivity to extremes of precipitation have tended to decline.

5. Our results provide novel insights about the impact of climate change on bird communities. Significant lagged effects highlight the potential for altered species' interactions to drive observed climate change impacts, although some community changes were driven by more immediate responses to warming. In England, resident and short-distance migrant populations have increased in response to climate change, but potentially at the expense of long-distance migrants, habitat-specialists and cold-associated species.

Keywords: birds, climate change, community specialisation index, community temperature index, migrants, population trends, precipitation, temperature.

Introduction

Climate change is projected to have a significant effect upon the future rate of biodiversity loss, the first consequences of which are already being detected (e.g. Parmesan & Yohe 2003; Thomas *et al.* 2004). There is mounting evidence for widespread changes to the distribution of species as a result of warming, with ranges spreading polewards and upwards (Hickling *et al.* 2006; Chen *et al.* 2011). Impacts of climate change have been detected on individual populations (e.g. Conrad, Woiwod & Perry 2002; Both *et al.* 2006; Foden *et al.* 2007; Wake 2007), although few studies have demonstrated increased risk of extinction in response to climate change (Cahill *et al.* 2013). Some of the strongest signals of climate change have been apparent at the community level (Morecroft & Speakman 2013), indicative of differential impacts of climate change on populations of different species. These may be used to infer potential variation in the sensitivity of different populations and species to future climate change, and therefore are worthy of further investigation.

Many of these studies have been conducted on well monitored bird populations, where three main trends in community change have been described. Firstly, long-distance migrants have declined more than resident or short-distance migrant species (Holmes & Sherry 2001; Sanderson *et al.* 2006; Yamaura *et al.* 2009). This has been attributed to a range of factors, but there is evidence that climate change may have driven at least some of this variation. For example, long-distance migrants now arrive later relative to spring temperatures on the breeding grounds than they used to, which may have population consequences (Both & Visser 2001; Møller *et al.* 2008; Saino *et al.* 2010; although see Johansson & Jonzén 2012), whilst their populations may also be affected by climate change on the wintering grounds (Newson *et al.* 2009a).

Variation in population trends have been attributed to differences in wintering (Thaxter *et al.* 2010; Jones & Creswell 2010), and breeding location (Ockendon *et al.* 2012; Morrison *et al.* 2013), and habitat (Both *et al.* 2010), each of which may be interpreted in relation to potential effects of climate change, as well as other factors.

Secondly, communities have become increasingly similar to each other (homogenised) as a result of populations of generalist species increasing relative to those of habitat specialists (Devictor *et al.* 2008a; Davey *et al.* 2012; Le Viol *et al.* 2012); findings which are apparent across a wide-range of taxa (Spear & Chown 2008; Winter *et al.* 2009). Whilst this may be attributable to a range of drivers associated with land-use and management change (e.g. Devictor *et al.* 2008a; Doxa *et al.* 2012), there is increasing evidence that generalist species with a broader niche breadth may respond more positively to warming than specialists (Davey *et al.* 2012; 2013).

Thirdly, variation in population trends between species at individual locations has been linked to the spatial association of each species to temperature. Populations associated with warmer temperatures (which tend to have southerly distributions) have increased in abundance relative to more northerly distributed species associated with cooler temperatures (Devictor *et al.* 2008b; Jiguet *et al.* 2010; Lindström *et al.* 2013). This has led to detectable changes in communities of both birds and butterflies across Europe, as measured by the community temperature index (Devictor *et al.* 2012), although some of the changes observed may also be linked to land-use change (Clavero, Villero & Brotons 2011; Barnagaud *et al.* 2012).

Combined, there is good evidence that populations of long-distance migrants, specialists and cold-associated bird species have declined in Europe (Sanderson *et al.* 2006; Devictor *et al.* 2012; Le Viol *et al.* 2012). However, there is a lack of understanding about the extent to which such changes may be directly attributable to climate change in Europe, or precisely which components of climate change may be responsible. Given differential patterns of warming and precipitation change in different seasons of the year (see Fig. 5), there is a clear need to understand more precisely to which components of climate change species' populations are responding, the likely ecological mechanisms driving these population responses, and how these mechanisms vary between species.

To do this, we analysed long-term national population time-series data of birds in England, in relation to variation in both temperature and precipitation measures through the year. Importantly, this is an avifauna where both distribution and community changes have previously been attributed to warming (e.g. Thomas & Lennon 1999; Davey *et al.* 2012; Devictor *et al.* 2012). Specifically, we examined the extent to which the observed community changes of declining long-distance migrants, community homogenisation and increasing community temperature index may be driven by variation in species' sensitivity to the weather variables by testing whether species' population responses to temperature and precipitation varied with respect to migratory strategy, habitat specialisation and thermal association. In order to identify the seasons where long-term climate change is most likely to have driven recent changes in bird populations, we then regressed long-term population trend against species' sensitivity to temperature and precipitation in each month.

Materials and Methods

DATA

Data from the British Trust for Ornithology's (BTO) Common Bird Census (CBC) and the BTO/Joint Nature Conservation Committee/Royal Society for the Protection of Birds Breeding Bird Survey (BBS) were used to generate annual indices of population change for England from 1966 to 2011. The CBC provided data from 1966 until 1994. Within the CBC, bird territories were mapped from observations made on seven to ten visits per year to self-selected sites (Marchant *et al.* 1990). The BBS involves two parallel 1km line-transects in 1km squares being surveyed during two early morning surveys between early April and late June (Gregory & Baillie 1998; Risely *et al.* 2012). These two methods produce differently structured data at the site level, making combined analysis at this resolution across the entire time-period very difficult. However, at the national level, despite the switch in methodology, the data from the two surveys can be combined to produce joint trends for most species using a log-linear model with a Poisson error distribution (Freeman *et al.* 2007). We therefore analysed data for 59 species (listed in Appendix S1) with comparable trends for England from both CBC and BBS that can be used to generate robust annual estimates of abundance using well-established analytical protocols developed specifically for this purpose (e.g. Gregory *et al.* 2005; Newson *et al.* 2009b). Trends were fixed to one in the first year (1966) and indicate relative population changes across species, so that each species contributes equally to the analysis.

Variation in the weather was described by monthly averages of temperature and precipitation for England (http://www.metoffice.gov.uk/climate/uk/datasets/). For the purposes of analyses, we focussed on mean monthly temperature (°C) and total

monthly precipitation (mm), although equivalent patterns in the data for temperature were also produced using mean minimum and mean maximum monthly temperatures (Appendix S2).

Given the strong spatial autocorrelations in weather variables and our use of national summaries of bird populations, this paper describes large-scale population responses to large-scale climatic variation. We do not consider how variation in the conditions experienced at individual sites (e.g. Newson *et al.* 2014), or local adaptation, might influence specific population responses.

STATISTICAL ANALYSIS

Annual variation in the population (*n*) growth rate of each species from year *t* to year t_{+1} ($\ln(n_{t+1}/n_t)$) was modelled as a function of each of the monthly weather variables, using a single model combining data from all species. Count (n_{t+1}) was modelled using a Poisson error distribution and a log link function, with $\ln(n_t)$ specified as an offset in order to generate the log-ratio of change. Count in the first year (n_t) was also included as a predictor variable to account for potential density-dependence and survey error (Freckleton *et al.* 2006). Species identity was specified as a random effect, and a first-order autoregressive function accounted for potential temporal autocorrelation in the data. The Kenward-Rogers correction was applied to ensure the correct estimation of the degrees of freedom. This model was run for temperature and rainfall separately.

We considered also correcting for relatedness amongst species in our analysis, to reduce the possibility of Type 1 errors arising from phylogenetic autocorrelation. The

inclusion of family identity as an additional random effect accounted for a negligible amount of covariance (mean across all models = $2.98E^{-20} \pm 5.41E^{-21}$) compared to that attributed to species (mean across all models = $0.011 \pm 7.99E^{-5}$). To further examine similarity of response between species as a function of relatedness, we repeated all analysis, but with species included as a fixed effect instead of a random effect, and then conducted a Moran's I test on the species effects in relation to their phylogenetic similarity. In only three cases was this test significant; models of the interaction between STI and temperature in $April_{t-1}$ ($P = 0.022$), $July_{t-1}$ ($P = 0.025$) and $April_t$ ($P = 0.049$). Given this lack of evidence for species population responses to temperature and precipitation being phylogenetically conserved, and given the statistical difficulties of accounting for phylogenetic independence within a single model that includes multiple observations from the same species that are temporally autocorrelated, we have not formally corrected for relatedness (see Kunin 2008).

For 11 % of tests, the inclusion of the autoregressive function led to a failure of model convergence, in which case the function was deleted. To assess the extent to which this may have reduced the comparability of these models with the remainder, we repeated the analysis without the autoregressive function for all models, and correlated the parameter estimates and standard errors from the two models for all cases where both were estimated. Parameter estimates and standard errors were virtually identical and highly correlated ($r > 0.993$ and 0.986 respectively), demonstrating that the model outputs were comparable. Nevertheless, we highlight these cases to the reader in case they are more susceptible to Type I error.

Whilst we used the mixed-model framework to estimate mean responses to each weather variable across all species, it was necessary to account for species-specific variation in the strength of density-dependence. Each model therefore included the species * n_t interaction. The final model was specified as follows, with *w* as the weather variable of interest, and a, b_o, and b_1 modelled estimates of the intercept, species-specific effect of density-dependence and mean weather effect size across all species, respectively.

$$ln\left(\frac{n_{t+1}}{n_t}\right) = a + b_0 sn_t + b_1 w + \varepsilon$$

We tested the effect of monthly weather variables from April in the year before the first survey ($April_{t-1}$) to June at the end of the second survey ($June_{t+1}$), a spread of two years plus three months of the second survey that allowed for some investigation of potential lagged effects of weather variables upon populations which have been shown to be important for some species (e.g. Pearce-Higgins *et al.* 2010), without over-inflating the number of variables considered (Fig. 1). These models provide a description of the mean sensitivity of the bird community as a whole to weather at different times of the year, and although not the main focus of this paper, are reported in Appendix S3, alongside additional models that test for potential non-linear relationships between weather variables and population growth through the inclusion of an additional term $b_2 w^2$ in the model.

Factors affecting variation in the sensitivity of different species.

The effect of these weather variables is likely to differ between species in a manner that can account for the observed changes in community composition. Therefore, the

focus of this paper is to test the extent to which species-specific responses to the weather varied with migratory strategy, habitat specialisation (niche-breadth) and thermal association. The pattern of these results indicate the likely processes underpinning each of the observed community responses to climate change. Species were classified as resident, short- and long-distance migrants from Thaxter *et al.* (2010). Niche breadth was measured using the species specialisation index (SSI), calculated from the coefficient of variation of species' density across habitats (Davey *et al.* 2012). Thermal association was summarised using the species temperature index (STI), calculated as the mean temperature across each species European breeding range (from Devictor *et al.* 2012). This test was achieved by separately adding to each model the each trait variable (*t*) plus its interaction with the relevant weather variable as follows.

$$ln\left(\frac{n_{t+1}}{n_t}\right) = a + b_0 sn_t + b_1 w + b_2 t + b_3 tw + \varepsilon$$

The three traits were independent (correlation between SI and STI values across species, r = -0.20, n = 59, $P = 0.11$; variation in STI, $F_{2,55} = 0.82$, $P = 0.44$ and SSI, $F_{2,55} = 1.08$, $P = 0.35$, with migratory strategy).

Variation in population trend with species' sensitivity to weather variables

In order to assess the extent to which species population trends may be related to their sensitivity to weather variables, and to directional shifts in those weather variables through time (climatic change), we estimated linear national population trends from the 45-years covered (1966-2011), from the slope of n_t against year. The interaction of this trend with species-specific responses to weather in each month was then tested, in

the same way as described for other ecological traits above. For example, a positive interaction with temperature in a particular month would show that species with a positive relationship between temperature and population growth in that month have generally shown a long-term increase. Similarly, species for which temperature had a negative impact on population growth will have tended to decline in abundance. In other words, we are testing the extent to which the effect of weather upon population fluctuations result in long-term population trends as a result of climate change.

All analyses were undertaken using PROC GLIMMIX in SAS 9.2 (Littell *et al.* 1996). Given the number of tests performed, we applied Bonferroni correction to highlight those which are most likely to be statistically significant and meaningful ($P < 0.00185$), and focus primarily on those in the discussion of the results, although record all of the weaker relationships for completeness. All parameter estimates, standard errors and significance values of relationships shown graphically are presented to the reader in Appendix S4.

Results

FACTORS AFFECTING VARIATION IN THE SENSITIVITY OF DIFFERENT SPECIES

Monthly variation in the mean temperature effect upon populations was generally similar between residents and short-distance migrants (Fig. 2a,b). Significant interactions between migratory strategy and winter temperature were apparent in $February_{t-1}$ ($P = 0.0021$), $December_t$ ($P = 0.0065$) and $January_t$ ($P = 0.0005$), although only the latter was below the Bonferroni threshold. These interactions are indicative of a strong positive effect of winter temperature upon populations of resident species

296 counted in the following spring, the significance of which exceeded the Bonferroni
297 threshold for residents for $December_t$, $January_t$ and $February_t$ (Appendix 4). The same
298 relationships were apparent, but weaker, in short-distance migrants, and not apparent
299 in long-distance migrants (Fig. 2c). The strongest interaction between temperature and
300 migratory strategy was with May_t temperature (P = 0.0003), which was particularly
301 related to population growth in resident species (0.00915 ± 0.0035), but negatively in
302 long-distance migrants (-0.0203 ± 0.0066), although neither effect achieved
303 Bonferroni significance. The strong contrast for $June_{t+1}$ temperature was between a
304 positive effect on long-distance migrants and negative impact on short-distance
305 migrants, neither of which achieved Bonferroni significance in isolation. Across
306 species, there was also evidence of a strong negative effect of summer temperature
307 with a one year lag ($July_{t-1}$ and $August_{t-1}$) upon population growth (Appendix S3),
308 which was below the Bonferroni significance level for both short-distance and long-
309 distance migrants for $July_{t-1}$. Variation in the response of populations to precipitation
310 did not differ strongly with respect to migratory strategy (Fig. 2d-f), and broadly
311 reflected the general patterns across species of positive effects of wet spring weather
312 in year $t_{-1,}$ particularly resident and short-distance migrants in $April_{t,}$ and of
313 precipitation in July and August in $year_{t-1}$ upon population growth. Resident species
314 also showed strong positive effects of precipitation in $October_t$ and $November_t$ upon
315 population growth (Appendix S3, S4).
316
317 The interaction between mean monthly temperature and SSI was statistically
318 significant (P < 0.05) for eight months, of which three remained significant after
319 applying the Bonferroni correction (Fig. 3a). All of these significant effects, and the
320 results for the majority of other months, were for negative interactions between

321 temperature and SSI, indicating that habitat specialists experience greater negative
322 impacts of warming than generalists. Although there was some evidence that the
323 previously detected lagged negative effects of summer warming were more severe for
324 specialists ($July_{t-1}$ $P = 0.003$, $August_{t-1}$ $P = 0.019$), the strongest contrasts were with
325 respect to spring temperature ($March_{t-1}$ $P = 0.0007$, $April_t$ $P = 0.047$, $March_t$ $P =$
326 0.0002, May_{t+1} $P = 0.0006$). Warmer spring weather tended to increase populations of
327 generalists relative to specialists, both with and without a time lag. With respect to
328 monthly precipitation, correlations between population growth and the interaction
329 with SSI was significant for six months (Fig. 3b), of which those with May_{t-1} ($P =$
330 0.0006) and $July_{t-1}$ ($P < 0.0001$) remained significant after applying the Bonferroni
331 correction. The latter re-enforces the suggestion that the negative effects of hot, dry
332 summer weather most strongly affect specialists.
333
334 The effect of STI on population responses to temperature were largely positive, such
335 that species with a high STI were more likely to have more positive relationships
336 between temperature and population growth (Fig. 4a), i.e. as expected, population
337 change of warm-climate species positively correlates with warmer conditions.
338 Thirteen of the interactions were significant ($P < 0.05$), including five which remained
339 after applying the Bonferroni correction. All related to spring or early summer
340 temperature ($April_{t-1}$ $P < 0.0001$, $April_t$ $P = 0.0002$, $March_t$ $P =< 0.0001$, May_{t+1} $P =<$
341 0.0001, $June_{t+1}$ $P =< 0.0001$), and indicates that a greater number of individuals from
342 species with a high STI are recorded both in and following warm breeding seasons.
343 Ten of the interactions between STI and precipitation also reached significance ($P <$
344 0.05), with negative correlations with $April_{t-1}$ ($P < 0.0001$), May_t ($P < 0.0001$) and

345 September$_t$ (P < 0.0001), and a positive correlation with March$_{t-1}$ (P < 0.0001)
346 remaining significant after applying the Bonferroni correction (Fig. 4b).
347
348 VARIATION IN POPULATION TREND WITH SPECIES' SENSITIVITY TO
349 WEATHER VARIABLES
350 There were strong and largely positive correlations between species' sensitivity to
351 temperature and population trend (Fig. 5a). A total of 16/27 relationships were
352 significantly positive, and a further two negative, whilst 11 positive interactions
353 remained signification after Bonferroni correction. The most consistent positive
354 relationships occurred in spring (April$_{t-1}$, March$_{t-1}$ to May$_t$ and March$_t$ to June$_{t+1}$),
355 although positive effects of summer (July$_{t-1}$ and to a lesser extent August$_{t-1}$), autumn
356 (November$_{t-1}$, November$_t$) and late winter (Februrary$_t$) temperature upon population
357 growth were also apparent. The months where there was the strongest interaction
358 between species' sensitivity to temperature and population trend were not those where
359 temperature appeared to have the strongest mean impact across species (correlation
360 between y-axes of Fig. S3ai and Fig. 5a; r = -0.20, P = 0.31), but were those where
361 the amount of warming had been greatest (correlation between y-axis and z-axis of
362 Fig. 5a; r=0.65, P = 0.00024).
363
364 Species sensitivity to precipitation was correlated with population trend across 11 of
365 the months covered, although for only two of these (April$_{t-1}$ and March $_{t-1}$) did these
366 achieve Bonferroni-corrected significance. Unlike temperature, there was no
367 correlation between the trend in precipitation and the interaction between population
368 growth and species' sensitivity to precipitation (r = 0.14, P = 0.49). Instead, mean
369 species' sensitivity to precipitation in that month (Fig. S3aii) was negatively

correlated with the relationship between precipitation sensitivity and long-term trend (r = -0.66, P = 0.00017). This indicates that in months where species responses to precipitation were largely positive, species with the most positive relationship between precipitation and population growth tended to decline. Similarly, in months where precipitation had largely negative effects upon population growth, species with the most negative relationship between precipitation and population growth tended to decline. In other words, species most sensitive to precipitation extremes were those with the most negative population trends.

Discussion

We have presented important evidence identifying the key periods of the year in which bird populations in England are affected by the weather, and how climate change may have driven recent changes in bird communities.

Firstly, three main periods of sensitivity were apparent across species; the breeding season (particularly June$_t$), winter (December$_t$ to February$_t$) and summer (July$_{t-1}$ and August$_{t-1}$), although the importance of different months varied between species groups. Positive relationships between winter temperature and population growth of resident and short-distance migrants reflect negative effects of cold winter weather on survival rates of many species, from small passerines, such as winter wren *Troglodytes troglodytes* and treecreeper *Certhia familiaris* (Peach, du Feu & McMeeking 1995; Robinson, Baillie & Crick 2007) to large waders such as northern lapwing *Vanellus vanellus* and Eurasian golden plover *Pluvialis apricaria* (Peach, Thompson & Coulson 1994; Piersma *et al.* 2005). Although for individual species, the duration of snow cover or the number of frost days may provide better predictors of

survival or population change (e.g. Greenwood & Baillie 1991; Robinson, Baillie & Crick 2007), our results suggest at the large scale, cold winters have a consistent negative impact upon resident and short-distance migrant breeding bird populations in England. Unsurprisingly, populations of long-distance migrants were unaffected by winter temperature during $year_t$, but instead are strongly correlated with rainfall on their wintering grounds (Peach, Baillie & Underhill 1991; Newson *et al.* 2009a; Pearce-Higgins & Green 2014).

Positive effects of June breeding season temperature are probably mediated through increased invertebrate food abundance, reduced thermoregulatory requirements and increased foraging time (Pearce-Higgins & Green 2014) associated with warm weather. These were most apparent in resident species, with strong relationships close to the Bonferonni threshold apparent also in $April_t$ and May_t. The strongly significant negative effect of May_t temperature on long-distance migrant population trends, in contrast to the positive effect on resident species, accounts for the less positive effect of May_t temperature overall on bird populations (Fig. S3a). This contrast is consistent with the proposed vulnerability of long-distance migrants to climate change on the breeding grounds, as a result of phenological mismatch. Late arriving, long-distance migrants that have failed to advance their arrival time have tended to decline in abundance, particularly in seasonal habitats (Møller *et al.* 2008; Saino *et al.* 2009; Both *et al.* 2010). Although the empirical evidence in support of detrimental impacts of mismatches on migrant populations in the UK is so far weak (reviewed in Pearce-Higgins & Green 2014), we would nevertheless expect May temperature to have positive impacts on resident species likely to be feeding chicks, but a negative impact on long-distance migrants likely to be incubating their eggs at this time, and therefore

unable to further adjust their breeding phenology to compensate for accelerated environmental conditions.

Detrimental impacts of hot, dry summers on bird populations, were apparent, but appeared to operate with a one-year lag. Thus, such conditions in $year_{t-1}$ will result in a population decline, not from $year_{t-1}$to $year_t$, but between $year_t$ and $year_{t+1}$. This is the effect previously identified for some upland birds as a result of negative impacts of summer temperature upon their invertebrate prey (Pearce-Higgins *et al.* 2010; Fletcher *et al.* 2013), and appears greatest in species that prey upon subsurface invertebrates whose larvae are vulnerable to desiccation, such as Diptera, and invertebrates which become less accessible in dry weather, such as Lumbricidae (Pearce-Higgins 2010; Carroll *et al.* 2011). Our results suggest that lagged negative impacts of hot, dry summer weather may affect more than just upland birds, and may be ecologically more important than more direct effects of summer drought that appear to affect post-fledging survival of thrushes (Robinson *et al.* 2004; Robinson, Baillie & King 2012). These conclusions emphasise the importance of research to identify the precise mechanisms which underpin these lagged effects, particularly as it is likely to be through such lagged impacts affecting ecological interactions that climate change may have the greatest impact on species' extinction risk (Cahill *et al.* 2013; Ockendon *et al.* 2014). The positive lagged relationship between precipitation in $April_{t-1}$ and population growth is less-clearly related to a specific mechanism, but may also influence trophic interactions, such as through changes in plant growth. The mechanisms underlying the positive effect of $autumn_t$ precipitation upon population growth, particularly apparent in October and November for resident species, was also

445 unclear, but may again occur through effects on other species, such as by influencing
446 prey availability during the winter.
447
448 Davey *et al.* (2012) suggested for Great Britain that increasing temperatures have
449 resulted in a reduction in community specialisation, a finding subsequently replicated
450 in Sweden (Davey *et al.* 2013). Our results are consistent with this observation, with a
451 generally negative interaction between mean monthly temperature and SSI (Fig. 3a).
452 Although these effects were not strongly tied to a particular month or season,
453 combined with the interactions for precipitation, they do suggest that negative effects
454 of hot, dry summers ($July_{t-1}$ and $August_{t-1}$) may be most apparent in habitat
455 specialists, whilst the positive effects of spring temperature ($March_{t-1}$, $April_{t}$) may be
456 greatest for generalist populations. Interestingly, the strongest interactions were for
457 $March_{t+1}$ and May_{t+1} temperatures, suggestive of a differential effect of breeding
458 season temperature upon the settlement or detectability of generalist and specialist
459 species. This is consistent with the observation that the strongest correlations between
460 temperature and community change are with breeding season temperature during the
461 year of the second survey (Davey *et al.* 2012, 2013). The meaning of more positive
462 effects of lagged May_{t-1} precipitation upon specialists than generalists (Fig. 3b) is
463 uncertain, but may be attributed to potential changes in vegetation growth and habitat
464 quality following wet springs that could enhance their breeding success and survival
465 (e.g. Robinson *et al.* 2004).
466
467 The analysis of interactions between species' responses to weather and thermal
468 association produced similar findings to those just described for habitat specialisation.
469 Thus, as expected from the large-scale increase in CTI observed across Europe

(Devictor *et al.* 2012), there was a tendency for positive interactions between STI and temperature effects on population growth across a range of months (Fig. 4a). Effects were strongest during the spring of the first survey ($March_{t-1}$ – May_t, although phylogenetic autocorrelation signalled the potential for a Type 1 error in the positive interaction in $April_t$). This suggests that warmer breeding seasons tend to increase the productivity of warm-adapted species, whilst warming during the spring of the second survey ($March_t$, May_{t+1} and $June_{t+1}$), may lead such warm-adapted species to either settle further north, or to be more detectable. Despite concerns over the role of land-use change in also influencing changes in STI (Clavero, Villero & Brotons 2011; Barnagaud *et al.* 2012), and potential uncertainty over the interpretation of CTI (for example, whether changes are caused by increases in warm-associated species, reductions in cold-associated species or both, or the fact that the breadth of the temperature niche does not influence a species' contribution to CTI), our results are consistent with the concept that changes in CTI track avian population responses to warming.

Finally, our results highlighted widespread correlations between long-term population trends and species' sensitivity to temperature, compared to precipitation. Thus, recent warming trends appear likely to have contributed to the observed changes in bird communities previously described, including declines in long-distance migrants, habitat specialists with a narrow niche breadth and cold-adapted species (Sanderson *et al.* 2006; Davies *et al.* 2012; Devictor *et al.* 2012). Although there was no match between the main periods of sensitivity to weather across species, and the periods of greatest correlation between sensitivity and population trend, it did appear that species whose populations had increased, tended to be those with positive relationships

between temperature and population growth in periods of greatest warming. In particular, late winter and spring warming appears to have caused increases in populations with significant positive relationships between $February_t$, $March_t$, May_{t+1} and $June_{t+1}$ temperatures and population growth. This potentially accounts for the apparent effects of conditions during $spring_{t+1}$ upon changes in both community specialisation and CTI. Long-term population trends did not appear significantly related to the periods of greatest contrast between species with differing migratory strategies, including May_t and $February_t$. In addition, the effect of precipitation upon long-term population trends was negatively correlated with mean precipitation effect, such that species which showed the greatest sensitivity to precipitation (having the most positive effects of precipitation upon population growth during periods where most species respond positively to precipitation, or the most negative effects of precipitation upon growth in months when most species respond negatively to precipitation), were also those which tended to decline. Although further work is required to fully attribute long-term population changes to climate change, our results suggest that both warming and changes in precipitation extremes may have influenced long-term avian population trends in the UK.

It is worth emphasising that the results presented here are for relatively common and widespread bird species monitored by extensive surveys. Although these data have previously formed the basis for assessing community level changes in response to climate change (e.g. Davey *et al.* 2012; Devictor *et al.* 2012), no very rare species, and few upland species, are sufficiently well covered by these surveys to be included in our analysis. Thus, as these other species may be particularly sensitive to climate change (Pearce-Higgins 2010), the results presented here may present a potentially

more positive overall assessment of climate change than would be apparent were the entire avifauna assessed. In addition, we have also not considered other potentially confounding non-climatic drivers of change that may also affect long-term population trends. Although these may be more responsible for some of the long-term trends observed than climate change (e.g. Eglington & Pearce-Higgins 2012), by including a first-order autoregressive function in our models, we significantly reduced the risk that our results may be due to Type I errors caused by other potential drivers of change being correlated with the precipitation and temperature variables.

To conclude, we have found good evidence that increasing winter and spring temperatures are likely to have improved climatic conditions for resident and short-distance migrant species in England, accounting for some of the observed long-term population increases in these species. A component of long-distance migrant population declines may also have been caused by warming in the UK, such as through increasing May temperatures, potentially through detrimental effects of phenological mismatch upon breeding success (e.g. Both & Visser 2001; Both *et al.* 2006) and lagged effects of hot, dry summers. The effects of such summer conditions were relatively widespread across species, particularly also affecting habitat specialists with a narrow niche breadth (Fig. 3a), and cold-adapted species (Fig. 4a), and may have been mediated through impacts on food resources reducing breeding success in $year_t$, as has previously been observed in upland habitat specialists (Pearce-Higgins 2010; Pearce-Higgins *et al.* 2010; Fletcher *et al.* 2013). Thus, our results add weight to the increased recognition of the need to consider potential lagged effects of climate change on species' interactions (Cahill *et al.* 2013; Ockendon *et al.* 2014). Finally, our results are consistent with previous work demonstrating negative impacts

of warming on habitat specialists with a narrow niche breadth (Davey *et al.* 2012, 2013) and northerly-distributed species associated with cold climates (Devictor *et al.* 2012). These community-level changes appear to represent the accumulation of consistent differential impacts of summer and spring warming. In summary, our analysis has provided novel insights about the climatic drivers of recently observed changes in bird communities in England than before, and strengthens the assertion that such changes are indeed at least partially a response to climate change.

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Data accessibility

The annual population trend estimates for England used in this paper can be viewed at http://www.bto.org/about-birds/birdtrends and are available through the BTO's standard data request procedure (see http://www.bto.org/research-data-services/data-services/data-and-information-policy).

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Fig. 1. Schematic illustrating the months and seasons over which weather data were collated (only every third month is shown for reasons of space) against the survey periods used to generate the population growth data. Vertical dashed lines indicate census years.

Fig. 2. Monthly variation in the mean effect of temperature (a-c) and precipitation (d-f) upon the population growth of bird species, plotted separately for resident (a, d), short-distance migrants (b, e) and long-distance migrants (c, f). Statistically significant ($P < 0.05$) interactions between weather variable effect and migratory status are indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni threshold for significance. The significance of individual effects are given in Appendix S4. Estimates from models in which the autoregressive function failed to converge, are circled as they may be more prone to Type I error.

Fig. 3. Monthly variation in the mean interaction (± SE) between temperature (a) or precipitation (b) and niche breadth (measured by the species specialisation index; SSI), upon the population growth of bird species. A negative interaction means that weather variables had a more negative, or less positive, impact on specialist than generalist species. Statistically significant interactions ($P < 0.05$) are indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni threshold for significance. Estimates from models in which the autoregressive function failed to converge, are circled as they may be more prone to Type I error.

838 **Fig. 4.** Monthly variation in the mean interaction (± SE) between temperature (a) or
839 precipitation (b) and thermal association (measured by the species temperature index;
840 STI), upon the population growth of bird species. A negative interaction means that
841 weather variables had a more negative, or less positive, impact on warm-associated
842 than cold-associated species. Statistically significant interactions ($P < 0.05$) are
843 indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni
844 threshold for significance. Estimates from models in which the autoregressive
845 function failed to converge, are circled as they may be more prone to Type I error.
846
847 **Fig. 5.** Monthly variation in the interaction between the relationship between weather
848 variables and population growth and 45-year population trends (solid line).
849 Statistically significant interactions ($P < 0.05$) are indicted by an asterisk, with those
850 outside of parenthesis achieving the Bonferroni threshold for significance. The single
851 circled estimate is from a model in which the autoregressive function failed to
852 converge, and may be more prone to Type I error. These are overlaid above the long-
853 term trend in weather variables (z-axis) for each month over the same period (grey
854 bars). Values vary slightly for the same month, depending on which year they refer to.
855 Error bars give standard errors.
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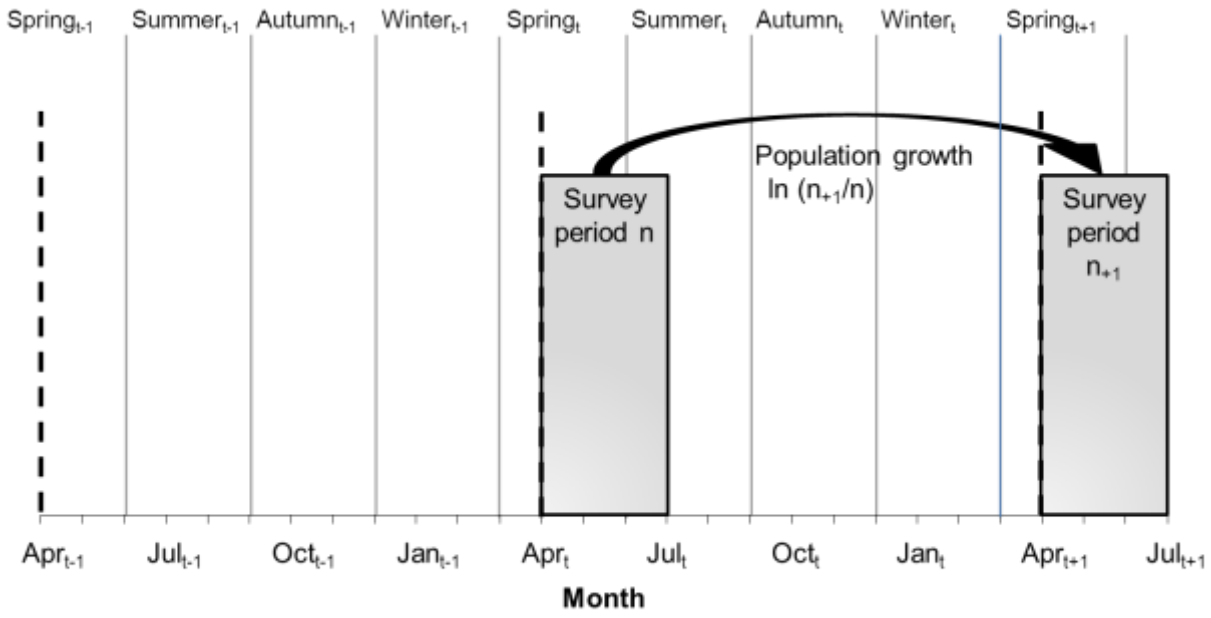
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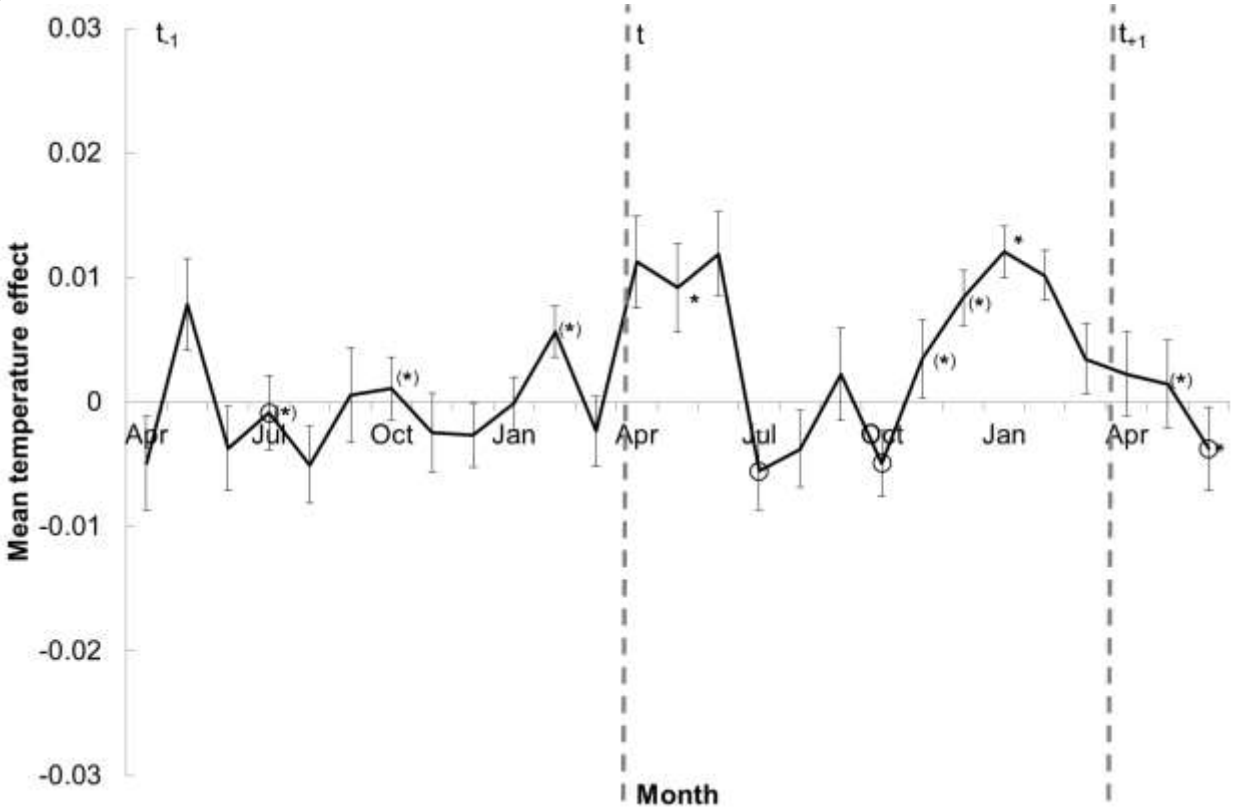
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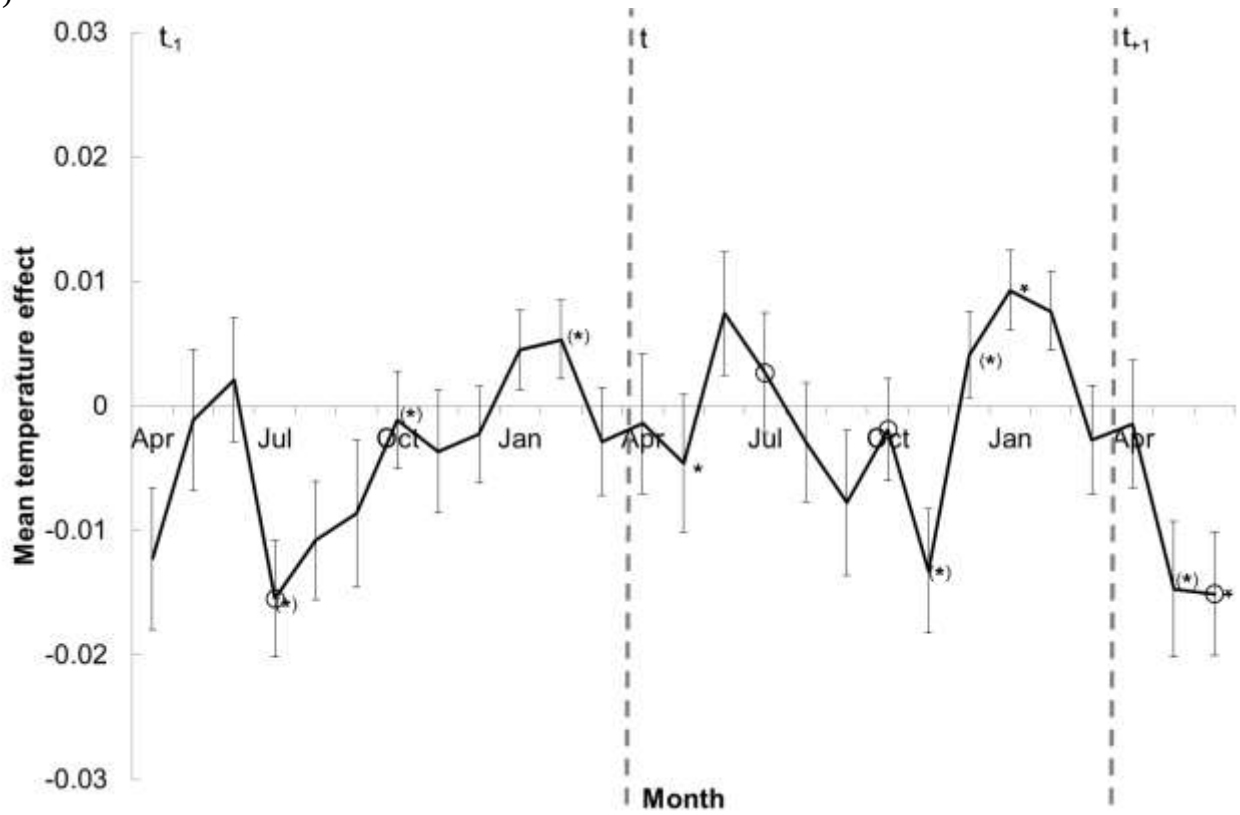
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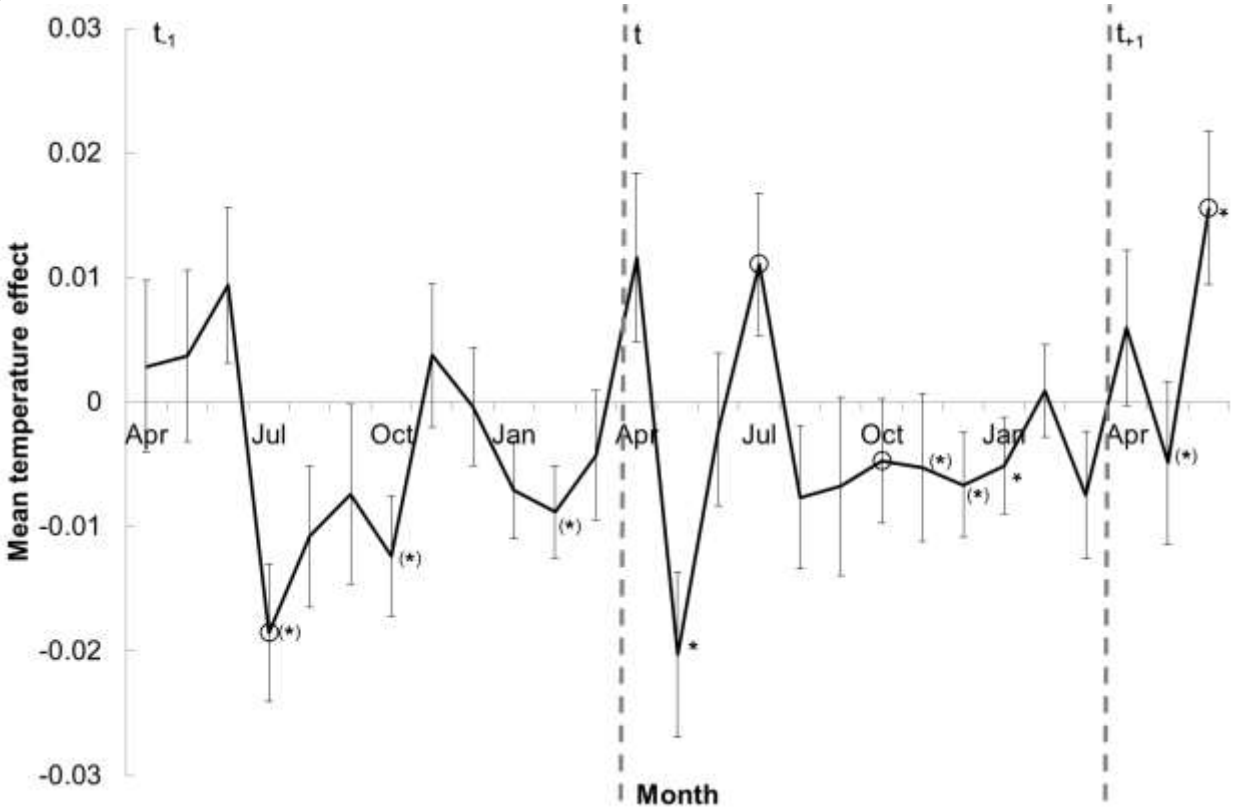

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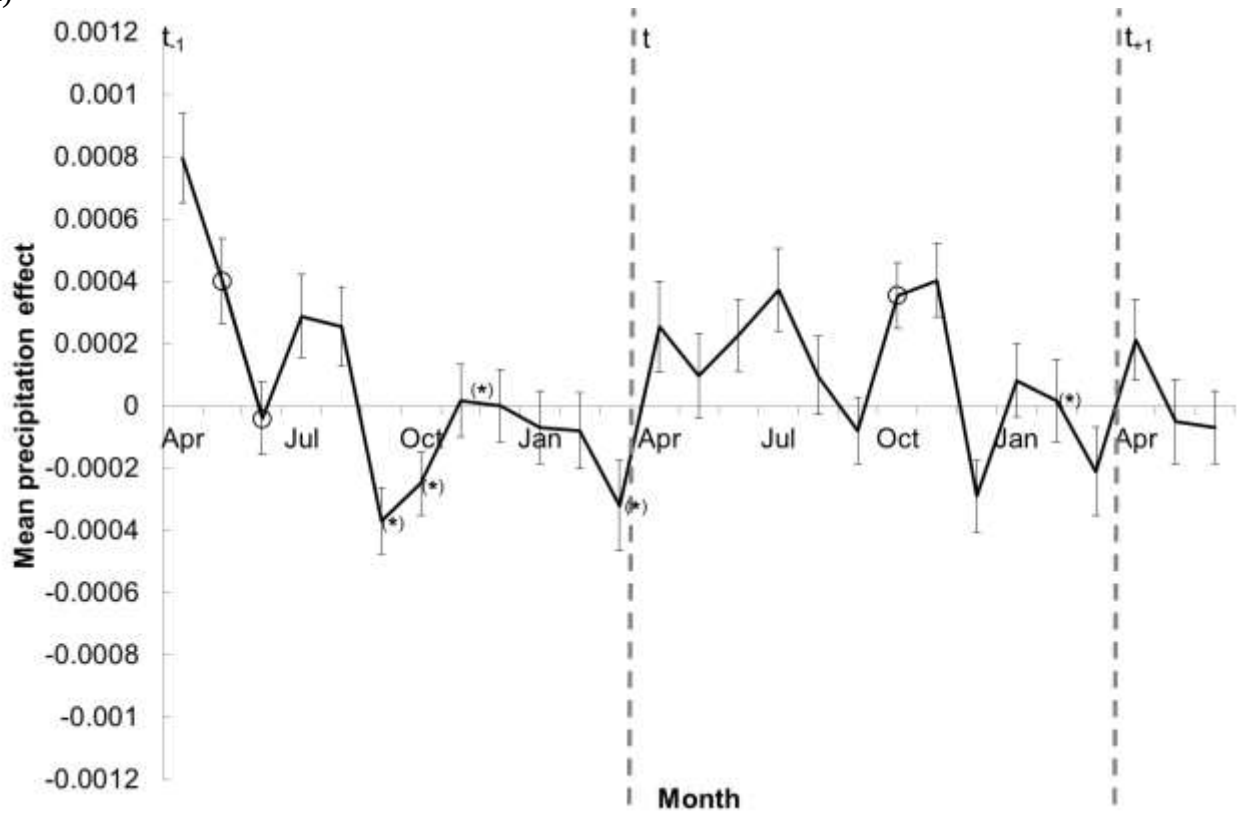

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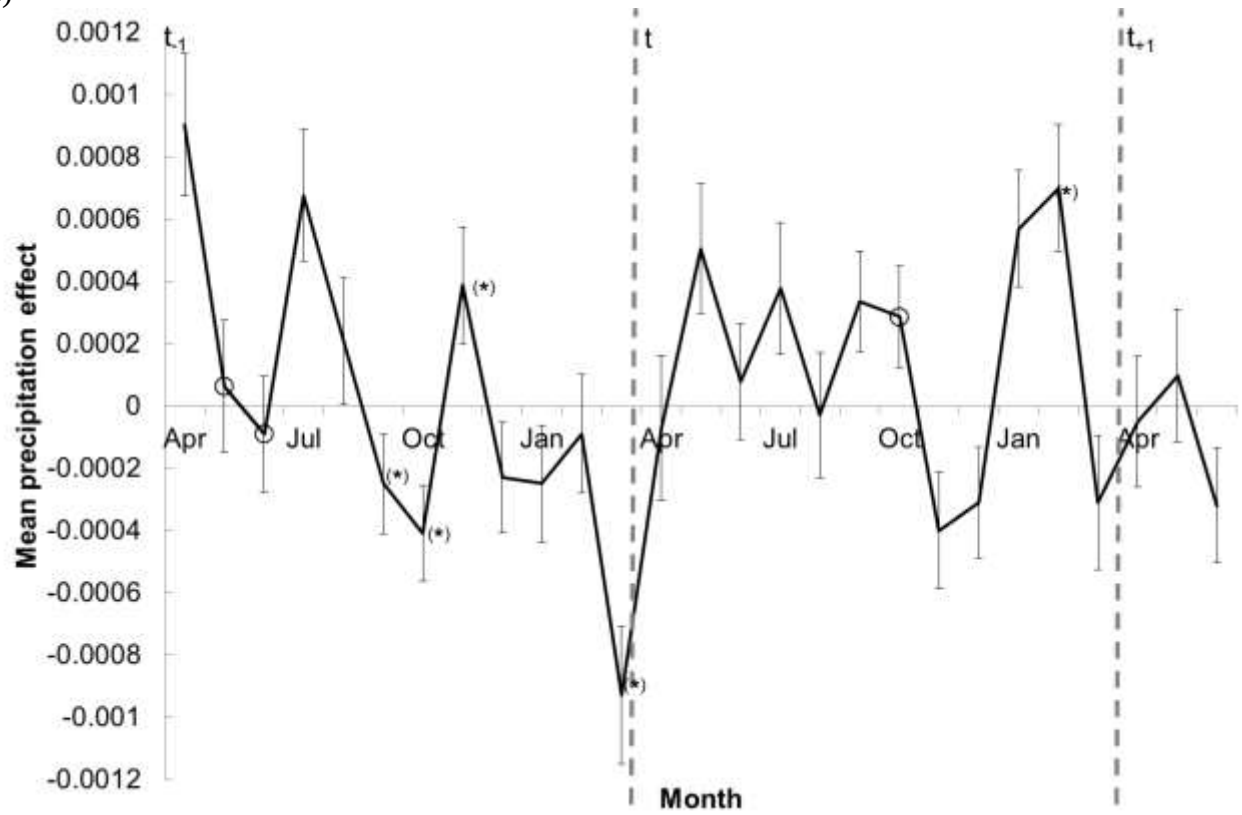

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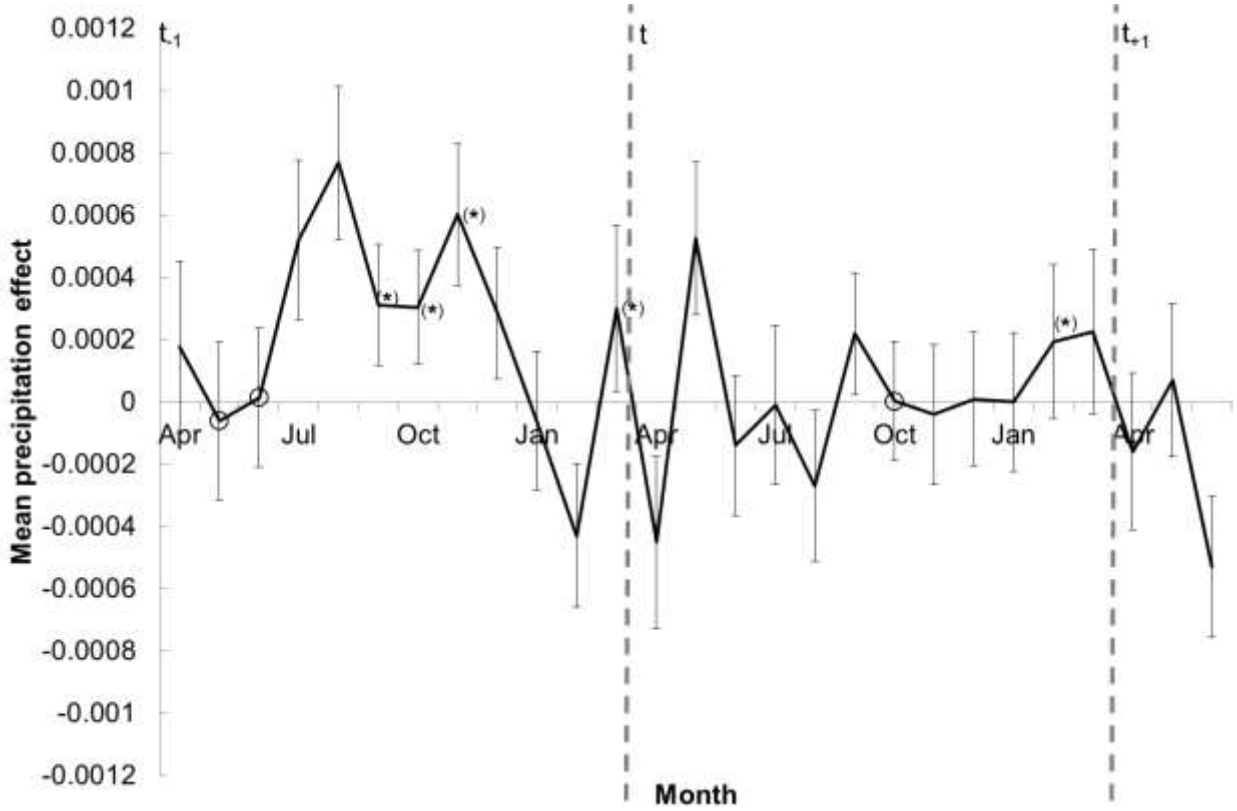

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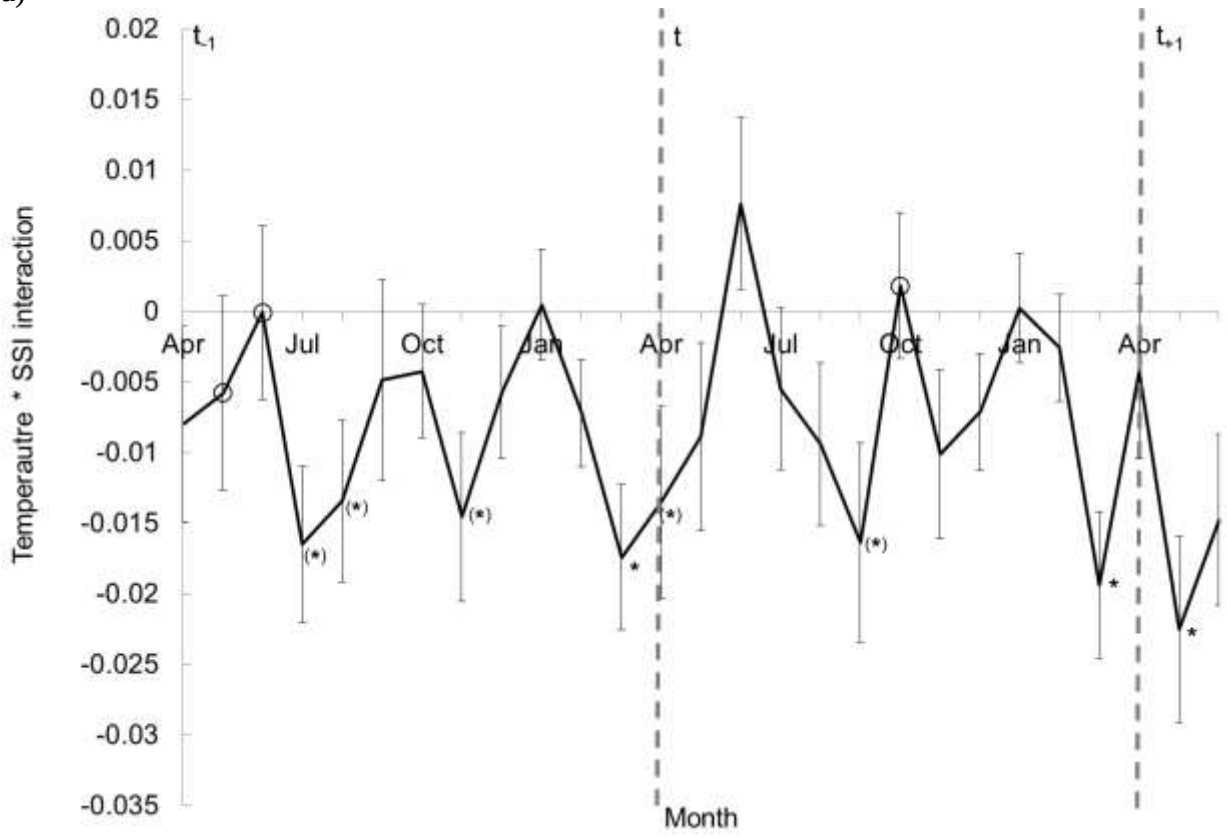

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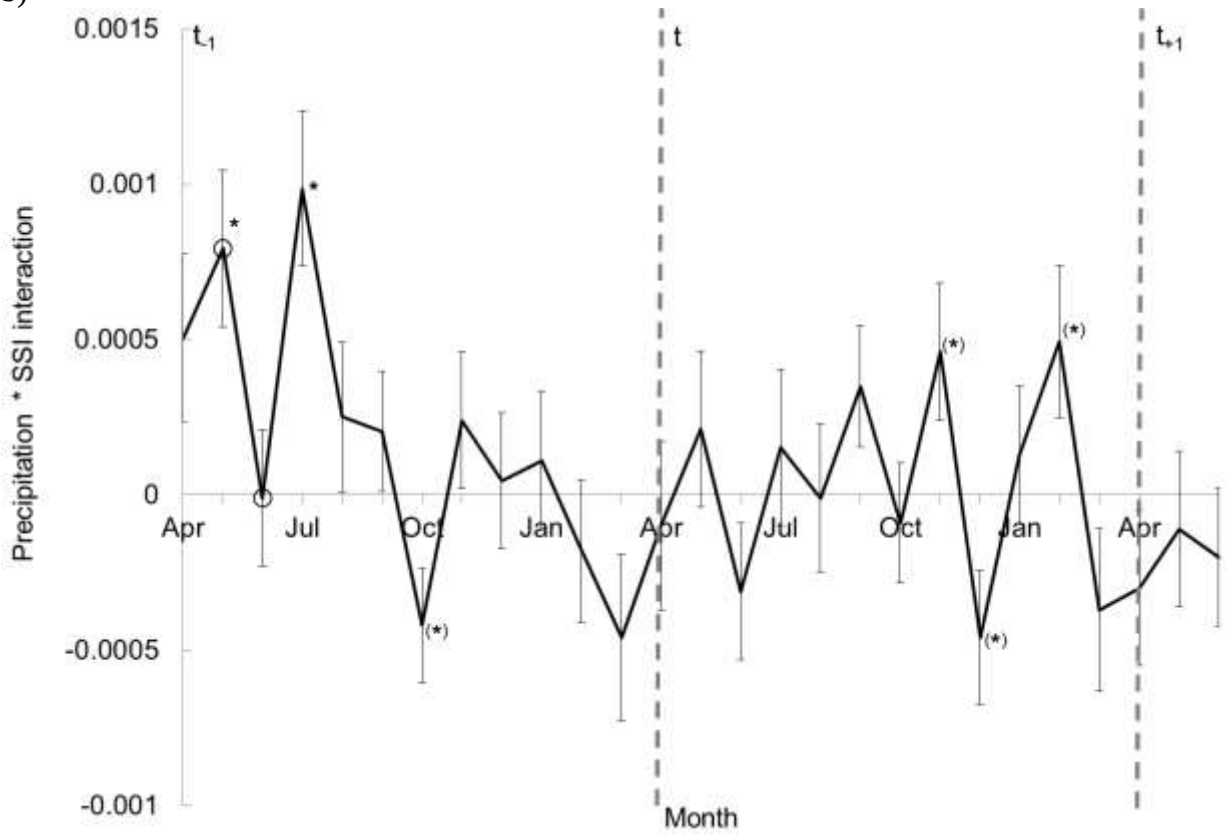

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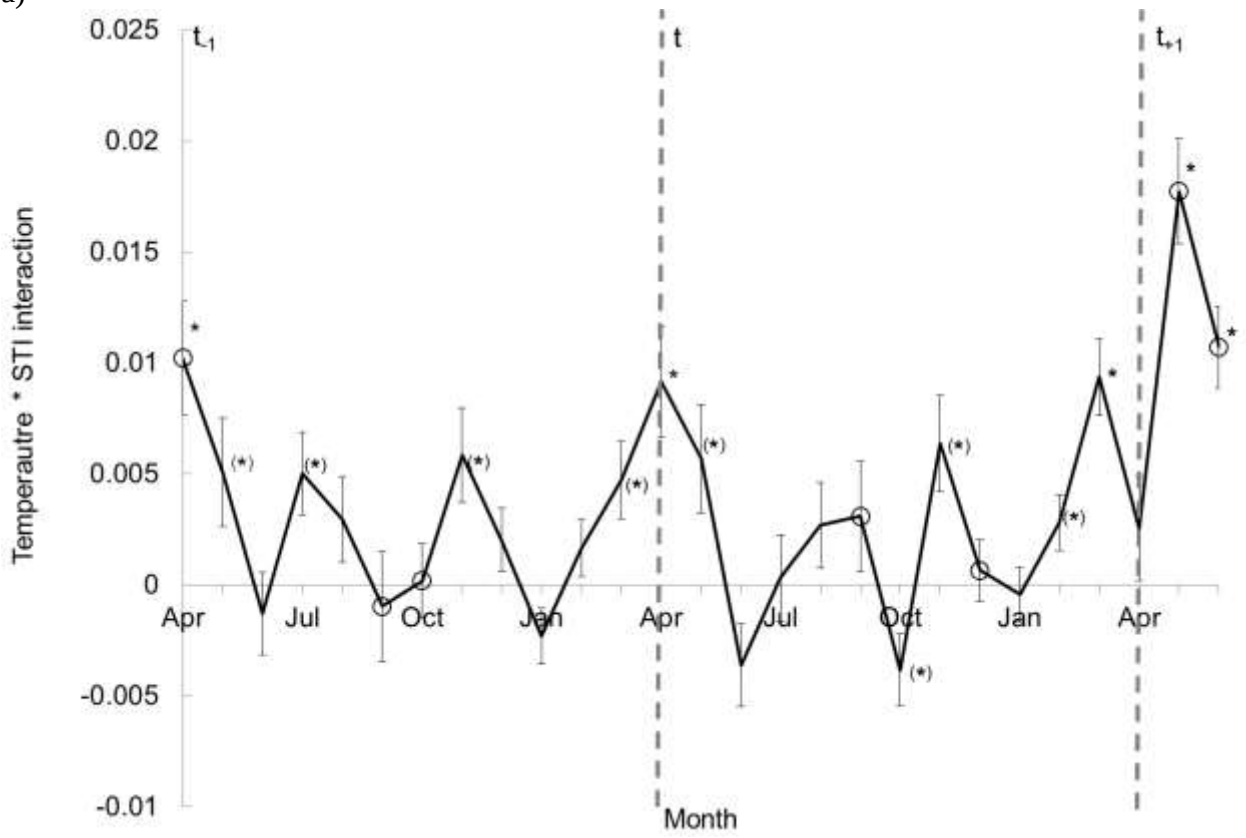
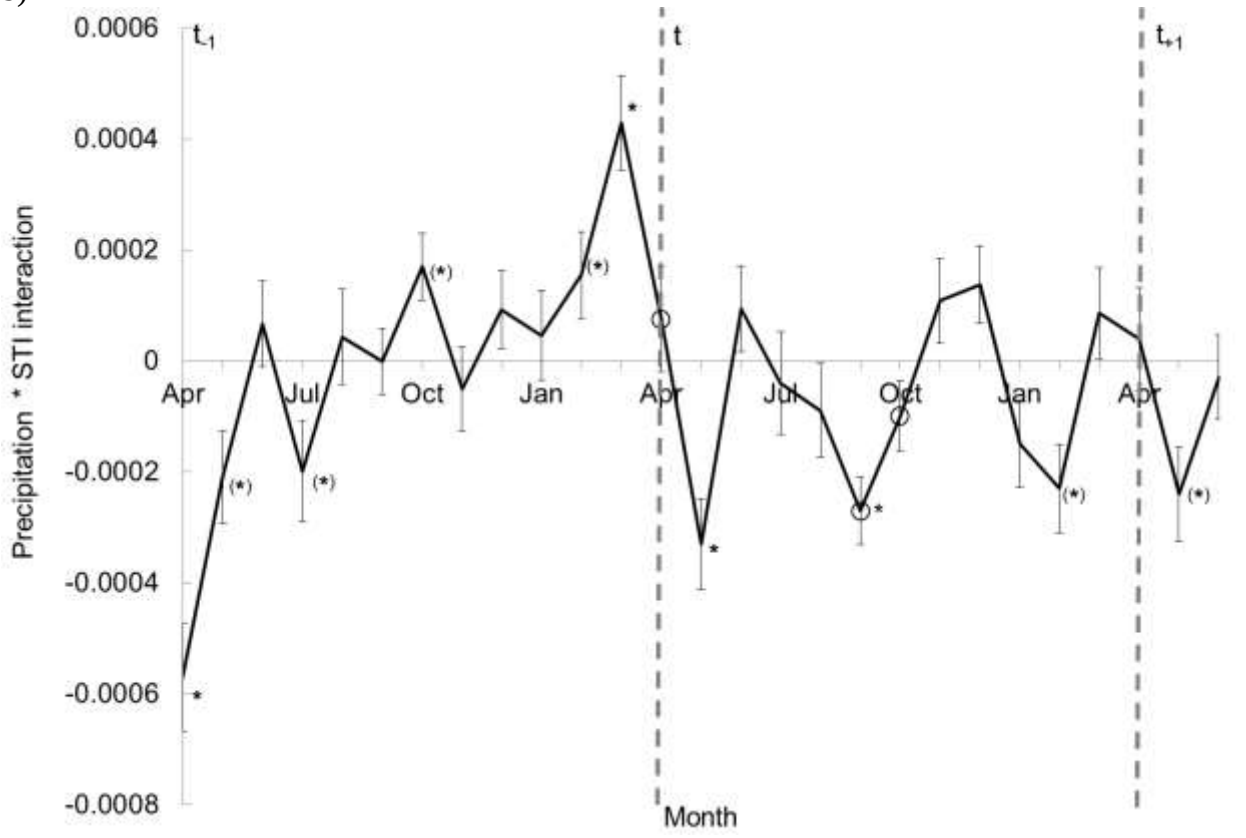


886
887 b)



888
889

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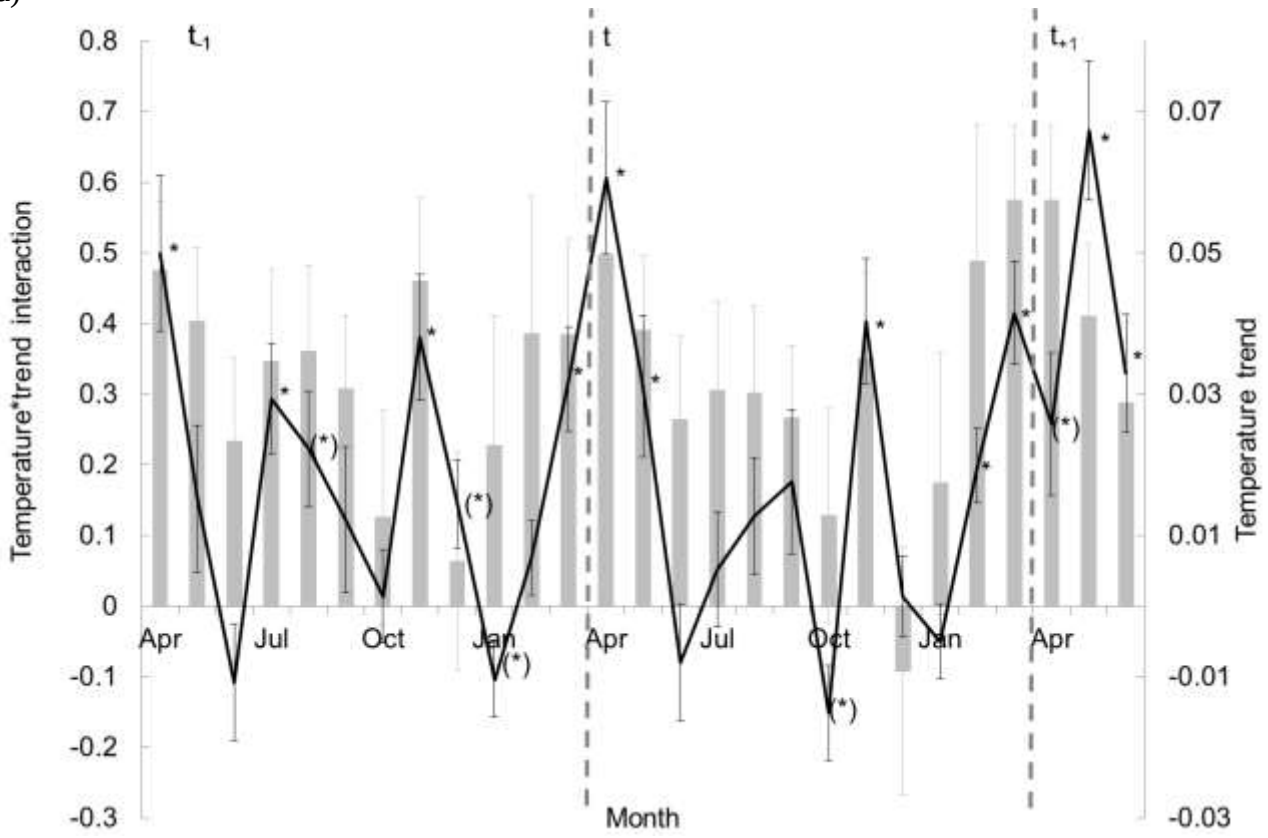
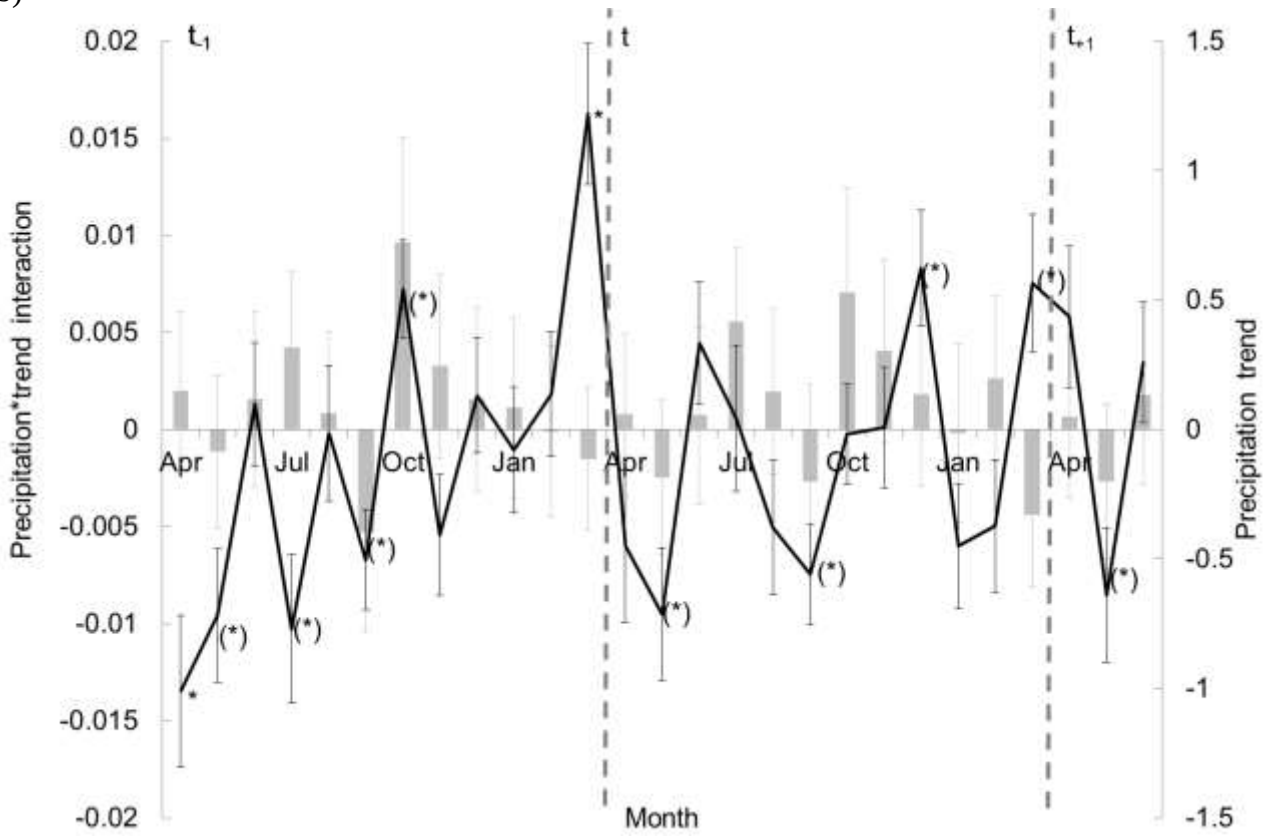


891

892 b)



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